



Optimal foraging, dietary change, and site use during the Paleolithic at Klissoura Cave 1 (southern Greece)



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ABSTRACT

This paper evaluates a long sequence of zooarchaeological remains from Klissoura Cave 1 (southern Greece) within the paradigm of evolutionary ecology. The prey choice, central place foraging, and patch choice models are applied to the dataset in order to understand subsistence shifts related to local resource depression and changes in the intensity of site use from the Middle Paleolithic through Mesolithic. Major trends in prey choice indicate that Middle Paleolithic hominins tended to focus on high-ranked large game resources, while Upper Paleolithic and Mesolithic occupants shifted to lower-ranked small game, fast-moving animals in particular. Overarching shifts in prey use do not correspond to environmental change, so they likely reflect human impacts on local prey populations. Reconstructions of body part profiles indicate that hunters exploited large game animals locally, possibly as they passed through the gorge or drank at a nearby stream. Occupation intensity at the site was highest at the beginning of the Aurignacian, which is reflected by an increase in material culture such as lithics and hearth features, as well as different subsistence strategies. Specifically, bone marrow processing is more important, evidenced by ungulate transport decisions that focus on marrow-rich elements, and an overall increase in marrow processing intensity. Environmental data indicate that conditions in southern Greece were particularly favorable at the beginning of the Aurignacian, which supported rich ungulate faunas and larger populations of their hominin predators in the area. In general, faunal data from Klissoura Cave 1 fit within larger trends found in the Mediterranean over the course of the Late Pleistocene, which indicate that human hunting pressures were on the rise. However, many aspects of prey use are specific to Klissoura Cave 1, reflecting unique environmental and cultural circumstances of southern Greece at various phases in the occupation of the site.

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1. Introduction

In recent years, the Greek Paleolithic has increasingly received much-needed attention from the archaeological community. Ongoing survey and excavation projects around the country, and the reanalysis and publication of previously excavated sites, allows archaeologists to ask more sophisticated questions about this period in Greece, addressing issues of site use, and shifts in cultural and economic strategies. The expansion of such datasets also facilitates the application of larger theoretical paradigms, in order to place Greece within the framework of social and demographic

change in the Mediterranean Basin during the Paleolithic. Much work needs to be done in the country, but projects in the Peloponnese (Daras and de Lumley, 1999; Douka et al., 2012; Farrand, 2000; Felsch, 1973; Harvati and Tourloukis, 2013; Harvati et al., 2003, 2013; Karkanas et al., 2004; Koumouzelis et al., 1996, 2010, 2001a,b; Panagopoulou et al., 2004; Perlès, 1987; Roger and Darlas, 2008; Stiner and Munro, 2011), northern Greece (Bailey, 1997; Bailey et al., 1983; Facorellis et al., 2001; Galanidou et al., 2000; Huxtable et al., 1992; Karkanas, 2001; Kotjabopoulou, 2001; Kyprissi-Apostolika, 2000, 1999), and on Crete (Strasser et al., 2010, 2011) are increasing our knowledge of this historically understudied region (Fig. 1).

Since its excavation in the mid-1990s through 2000s, Klissoura Cave 1 has contributed significantly to our understanding of the Paleolithic period in Greece. The site preserves a long archaeological sequence that spans the Late Pleistocene (ca.

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Fig. 1. Map of Greece showing key Paleolithic sites.

100,000–10,000 BP) and includes large Middle and Upper Paleolithic components, as well as a thin Mesolithic layer. Abundant archaeological materials recovered from the site provide the potential for evaluating long-term technological and behavioral shifts through the sequence, and addressing questions of changes in site use and local population fluctuations. Key to understanding Paleolithic lifeways is reconstructing variation in hominin diets. Many aspects of subsistence strategies at the site are discussed in previous works, with a focus on later time periods (Koumouzelis et al., 2001a; Starkovich, 2009; Starkovich and Stiner, 2010), or on shifts in the exploitation of a certain species or group of animals at the site (Starkovich, 2012a, 2012b). This paper seeks to evaluate the long sequence of faunal materials from Klissoura Cave 1 within the paradigm of evolutionary ecology. Specifically, the prey choice, central place foraging, and patch choice models are applied to the dataset in order to understand shifts in subsistence related to changes in the intensity of site use, and local resource depression over the course of the site's occupation.

2. Theoretical background

Changes in human diets may be influenced by a number of external factors, such as climatic shifts, or internal variables like population growth, reorganized landscape use, and changes in site occupation intensity. Evolutionary ecology is a useful paradigm for approaching questions about shifts in hominin subsistence patterns (see review in Bird and O'Connell, 2006; Lupo, 2007). The foraging models within this paradigm are based on the premise that organisms optimize their foraging efforts and reproductive success in order to maximize their fitness within a given environment (Pianka, 2000). Some optimality models that seek to explain foraging decisions include the prey choice model (Pianka, 2000; Stephens and Krebs, 1986), patch choice models (MacArthur and Pianka, 1966), and central place foraging models (Orians and Pearson, 1979; Schoener, 1979). Other models are also included under the umbrella of evolutionary ecology (e.g., costly signaling theory and tolerated theft). This latter set is excluded

from this discussion as the three previously mentioned models are more readily applied to the archaeological record of the Paleolithic.

Many authors studying the late Pleistocene of the Mediterranean Basin observe an intensification of food resources, particularly across the Upper Paleolithic (Atici, 2009; Bar-Oz and Munro, 2005; Hockett and Haws, 2009; Jones, 2009; Munro, 2004; Speth and Clark, 2006; Speth, 2004; Stiner and Munro, 2011; Stiner et al., 2000; Stiner, 2005, 2003, 2001; Tortosa et al., 2002). These shifts are often attributed to increased human population pressures, or cultural and technological changes. In this paper, optimal foraging models are utilized to test the hypothesis that intensification occurred on two different scales at Klissoura Cave 1. The first relates to periodic increases in site occupation intensity, which were likely driven by favorable local environments. The second is that foragers occupying the site experienced long-term resource depression as a result of regional population growth. I begin by discussing the three models in turn, before presenting a set of tests to evaluate these hypotheses.

2.1. Prey choice

The prey choice, or diet breadth, model is particularly useful for understanding dietary change among foragers (Pianka, 2000; Stephens and Krebs, 1986). Central to the prey choice model is the ranking of prey items according to their return rate. Return rate is based on the caloric or other nutritional value (e.g., fat) of a resource per unit of time spent obtaining it and post-encounter handling costs (Pianka, 2000; Stephens and Krebs, 1986). Unlike patch choice models (see below), the prey choice model assumes that resources are encountered randomly and sequentially on the landscape. Following this model, foragers seek to maximize their net caloric return by pursuing prey with the highest return rates whenever they are encountered. Conversely, low-ranked species are only pursued as high-ranked resources become scarce, regardless of the abundance of low-ranked food items in an environment (Emlen, 1966; MacArthur and Pianka, 1966; Pianka, 2000; Stephens and Krebs, 1986).

Ethnographic studies that employ prey choice models to understand human hunting decisions find that prey ranking is closely tied to body size, with larger taxa assigned a higher rank than smaller species (Broughton et al., 2011; Hames and Vickers, 1982; Hawkes et al., 1982; Hill and Hawkes, 1983; Kelly, 1995; Simms, 1987; Smith, 1991), as long as they are not too dangerous to procure or time-consuming to catch and process (Bird et al., 2009, 2012; Jones, 2004a; Smith, 1991; Ugan and Byers, 2005). This holds true for foragers in different environments, using a range of technologies to assist hunting efforts. Though small-bodied taxa are generally classified as low-return because they offer a smaller nutritional package than large game (Broughton, 1994a, 1994b, 1999), early designations of small prey did not necessarily take into account differences in handling costs within this broader category.

Stiner and colleagues (Munro, 2004; Stiner and Munro, 2002; Stiner, 2001; Stiner et al., 1999, 2000), as well as others (Morin, 2012:32–33; Steele and Klein, 2009), have argued that small game animals vary considerably in terms of capture costs and return rates, based on fundamental differences in their predator avoidance tactics. Therefore, some small game species likely have much higher rankings than others. For example, small, slow-moving taxa (e.g., limpets and tortoises) have much lower capture costs than small, fast-moving animals (e.g., hares, birds, and fish), even though their caloric yields are similar. The efficient procurement of small, fast-moving taxa is often not straightforward, requiring the cooperation of a large group of people for game

drives, or involving a significant technological and time investment into the manufacture and upkeep of snares and nets (Cannon, 2000; Jones, 2006; Lupo and Schmitt, 2002; Madsen and Kirkman, 1988; Madsen and Schmitt, 1998; Schmitt et al., 2004, but see Ugan, 2005). The higher search and handling costs for small, fast-moving game translate into a lower return rate as compared to similarly-sized slow-moving animals, so the latter should be preferentially exploited by human hunters (Stiner, 2001; Stiner et al., 2000), a fact that is largely supported by ethnographic data (Kelly, 1995; Kuhn and Stiner, 2001: Table 5.1).

A key application of prey choice models addresses the question of resource depression, which occurs when harvesting pressures lead to a decline in prey capture rates (Charnov, 1976). Archaeological studies that employ prey choice models often focus on resource depression (e.g., Broughton, 2002, 1999, 1997, 1994a, 1994b; Butler and Campbell, 2004; Butler, 2001, 2000; Cannon, 2000; Grayson and Delpech, 1998; Hill, 2007; Jones, 2006, 2004b; Manne and Bicho, 2009; Munro, 2004; Nagaoka, 2002a, 2002b, 2001; Speth and Clark, 2006; Speth, 2004; Stiner, 2001, 2005, 2009; Stiner and Munro, 2002, 2011; Stiner et al., 2000, 1999; Ugan, 2005), because resources in an assemblage are easily ranked and can be tracked diachronically as prey species are added to or removed from the list. Information on the diminution of prey size can also be used to independently check these interpretations (Speth and Tchernov, 2002; Steele and Klein, 2005–2006; Stiner et al., 2000). Resource depression may be linked to local environmental change or larger climatic shifts, but can also result from human factors such as intensification driven by increased human population densities. It is critical to rule out environmental factors before attributing resource depression to human activities.

2.2. Central place foraging

Central place foraging (CPF) models were first developed by ecologists to understand transport decisions by non-human animals that move food resources to a home base (i.e., central place) in order to feed without interference, store resources, or provision offspring (Orians and Pearson, 1979; Schoener, 1979). The key goal of this set of models is understanding how foragers choose patches, select prey, and determine load size for transport (Orians and Pearson, 1979). The models predict that as distance between the home base and resource patch increases, load size also increases to make travel costs worthwhile (Orians and Pearson, 1979; Schoener, 1979). This simple prediction appears to be valid for many non-human predators (see Stephens and Krebs, 1986:194–197), and CPF models were readily adopted by anthropologists, as the movement of resources to a central place is a fairly typical behavior for recent humans.

The widest use of CPF models in anthropology are studies that explore the butchery and transport decisions surrounding the processing and movement of vertebrate remains from a kill site to home base (Binford, 1978; Bunn et al., 1988; Egeland and Byerly, 2005; Lupo, 2006; O'Connell and Marshall, 1989; O'Connell et al., 1988; O'Connell et al., 1990). These ethnographic works establish nutritional values of different body parts and tissue types for various prey species in a range of habitats, from the arctic to tropics. The studies illustrate the wide range of variation in carcass transport decisions made by modern foragers depending on the prey species, number of participants involved in the hunt or transport effort, distance between the kill and habitation site, available technology, and local environmental conditions. This variation must be kept in mind when the outcomes of such studies are applied to the archaeological record. For example, in applying CPF models it is important to consider the fact that meat might not be the main goal of the foraging excursion. In some

instances, such as during the winter or periods of resource stress, nutritious bone marrow might be a more important outcome of a foraging foray.

Archaeological applications of CPF models follow the general trend in ethnographic research: seeking to understand the transport decisions of past foragers moving specific portions of large-bodied prey species (Broughton, 1999; Cannon, 2003; Faith and Gordon, 2007; Faith, 2007; Faith et al., 2009; Nagaoka, 2002a, 2005; O'Connell and Marshall, 1989; O'Connell et al., 1988; O'Connell et al., 1990; Speth and Scott, 1989; Speth, 1991). These studies conclude that as local resources are depleted, hunters travel farther from a home base site to procure large game animals. If meat is carried over long distances, hunters typically focus on transporting fewer high-utility skeletal elements (Broughton, 1999; Cannon, 2003; Nagaoka, 2005; Speth and Scott, 1989; Speth, 1991; Stiner, 1991, 1994, 2005). These applications are often used to evaluate intensification efforts and the depletion of local resources often brought on by human hunting pressures. The range of archaeological examples illustrates the utility of applying CPF models to sites from diverse time periods and geographic regions. The underlying assumptions allow for a quantitative evaluation of changes in body part transport strategies through an archaeological sequence.

2.3. Patch choice

The patch choice model, developed by MacArthur and Pianka (1966), is similar to the prey choice model, except it assumes that resources are encountered in discrete patches, as opposed to being evenly distributed across the landscape. Patches are encountered randomly and sequentially in a given environment and are ranked based on their return rate (Kelly, 1995). Once a forager enters a patch, the return rate drops as resources are depleted (Charnov, 1976). A benefit of the patch choice model is that the patches can be broadly defined: the distribution of a single species (e.g., raspberry bushes), an ecosystem (e.g., marine), or a foraging strategy (e.g., large game hunting) (Lupo, 2007).

An application of the patch choice model particularly relevant to this discussion explores the intensity with which individual animal carcasses are processed. In this case, the model is used similarly to examining patches on the landscape, with a different scale of analysis. Patches are defined as individual carcasses; foragers make decisions about how intensively to process each carcass, or patch, before moving on to the next kill (Burger et al., 2005; Nagaoka, 2005). Carcasses can logically be divided into higher and lower-return resources as animal tissues vary considerably in their nutritional return, based on both caloric value and on the effort needed to extract the resource. In general, organ and muscle tissue provide the highest returns, followed by bone marrow, and finally bone grease (see values in Binford, 1978; Kooyman, 1990; Lupo, 2006; Madrigal and Holt, 2002 for some examples). Foragers should only process labor-intensive bone grease if the returns are higher than the combined travel and handling costs of seeking the next kill. This might occur during periods of long-term resource depression, or possibly on a seasonal basis in regions with large temperature shifts and changes in resource availability (but see Lupo et al., 2013). Many zooarchaeological studies have explored the intensity of bone marrow or grease processing as a response to resource depletion and intensification efforts (e.g., Audouze, 1987; Audouze and Enloe, 1991; Bar-Oz and Munro, 2005; Brink, 1997; Broughton, 1999; Burger et al., 2005; David and Enloe, 1993; Ege-land and Byerly, 2005; Hill, 2007; Manne and Bicho, 2009; Nagaoka, 2005; Potter, 1995; Stiner, 2003; Weniger, 1987), though they do not all explicitly frame their studies within the patch choice model.

Each of the models discussed above can be used to address different aspects of the question of long-term or temporary intensification efforts at Klissoura Cave 1. Specifically, the prey choice model is applied to evaluate changes in the proportions of high- and low-ranked taxa at the site. Patch choice models are used to examine shifts in butchery patterns (i.e., marrow processing), and central place foraging models are employed to explore body part transport decisions. Evidence from elsewhere in the Mediterranean Basin indicates that human population densities were on the rise over the course of the Middle and Upper Paleolithic (Lahr and Foley, 2003). If this growth occurred, it must have increased human predation and subsequently stressed prey populations. In this context, resource intensification or depression should be reflected in hominin subsistence strategies. Expanding diets at Klissoura Cave 1 may be reflected by 1) an increase in low-return prey types, such as difficult to catch hares and birds, 2) an increase in high-utility ungulate body parts as hominins are forced to hunt further from the site, and 3) more intensive processing of carcasses, including the opening of marrow-poor elements. Investigating these issues will help determine if foragers at Klissoura Cave 1 experienced resource depression due to the long-term effects of population growth and environmental change, or more periodic shifts that might reflect changes in site occupation intensity. Before delving into the data itself, I review some critiques of evolutionary ecology.

2.4. Criticisms and responses

The application of evolutionary ecology to understand human foragers in the ethnographic and archaeological record has received a number of criticisms over the years (e.g., Dwyer, 1985; Joseph, 2000; Martin, 1983; Pyke, 1984; Smith, 2009; Zeder, 2012), and an equal number of thorough responses (Broughton and O'Connell, 1999; Smith and Winterhalder, 1985; Smith, 1991, 2000; Winterhalder and Smith, 2000; Winterhalder, 2002). These critiques have offered valuable points that help evolutionary ecologists strengthen their inquiries and refine their methods. One misgiving that is often voiced is the difficulty associated with applying mathematical models to human behavior. Indeed, it is unsettling to think that humans follow mechanistic behavioral models, as this seems to deny us free will or cultural preference. To this point, the benefit of models from evolutionary ecology is that they serve as a framework or baseline set of predictions for how we expect foragers to behave if they have a rational set of goals. The most interesting cases are the ones that unveil deviations from expectations set forth by optimality models, as these are often the places where biological needs and culture diverge.

A second, more practical criticism is how to define the currency used to test optimality models. Evolutionary ecologists tend to focus on kilocalories as the unit of measurement in foraging pursuits, but other nutritional factors (e.g., fat yields) may actually be of greater importance. In addition, the goals of a foraging foray may change depending on who is seeking food, for example a mother provisioning offspring. These issues are addressed extensively in the ethnographic literature (e.g., Bird and Bliege Bird, 1997; Hill and Hawkes, 1983; Hill et al., 1987; Kelly, 1995; Smith, 1991), but they are difficult to explore in the archaeological record because there are so many unknown variables. In most archaeological applications, prey mass is used as a proxy measure of kilocalories, though archaeologists acknowledge that these are only estimations.

Some recent criticisms of evolutionary ecology come from proponents of niche construction theory. These scholars assert that applications of evolutionary ecology rely too heavily on resource depression and demographic change in explaining subsistence shifts, and suggest that archaeologists should instead focus more on

the active role humans take in shaping their environments to achieve desired outcomes (Smith, 2009; Zeder, 2012). Other proponents of niche construction theory see no conflict between the two paradigms, arguing that they are complementary frameworks for understanding human–environment interactions (Broughton et al., 2010). While it is true that humans modify their environments regardless of their social organization or population density, I tend to agree with the latter set of authors that niche construction theory and evolutionary ecology are two sides of the same coin. In any case, environmental modifications are much more extreme in situations where population densities are higher or humans are sedentary; lifeways which did not begin until the end of the Pleistocene. Thus, applying models from evolutionary ecology to Middle and Upper Paleolithic hominins is entirely appropriate.

3. Klissoura Cave 1

Klissoura Cave 1 is located in the Klissoura Gorge of north-eastern Peloponnese (Fig. 1). The gorge is comprised of a system of karstic limestone caves that were periodically occupied during the Pleistocene and Holocene (Koumouzelis et al., 2001a). Though several of the caves preserve human activity, Klissoura Cave 1 has by far the most substantial record of human occupation (Koumouzelis et al., 1996). Klissoura Gorge is about 3 km long, connecting the Argive Plain to the south with the Berbati Valley in the north. A perennial stream drained the gorge during the Pleistocene. The combination of water resources and location at the interface between multiple ecological zones attracted diverse animal species and human foragers to the area. Today, the region has a typical Mediterranean climate, with cool, wet winters and warm, dry summers (Blondel and Aronson, 1999).

The caves in the Klissoura Gorge were recorded during the comprehensive 1988–1990 Berbati-Limnes archaeological survey (Koumouzelis et al., 1996). Excavations of the Upper Paleolithic and Mesolithic layers were directed by Margarita Koumouzelis of the Ephory of Paleoanthropology and Speleology in Athens, and Janusz Kozłowski at the Jagiellonian University in Krakow, Poland (Koumouzelis et al., 1996). Along with Panagiotis Karkanas, Koumouzelis expanded the excavation to include more of the Upper Paleolithic, as well as substantial Middle Paleolithic deposits. In total, the excavation included about five meters of anthropogenic deposits, which are divided into fourteen stratigraphic units based on geoarchaeological and archaeological layers (Kaczanowska et al., 2010; Karkanas, 2010; Sitlivy et al., 2007). Of the fourteen layers, one is Mesolithic, seven are Upper Paleolithic, and six are Middle Paleolithic in origin (Table 1). The sediments of the Upper Paleolithic and Mesolithic are primarily anthropogenic, while the Middle Paleolithic has a large natural input (Karkanas, 2010). Cultural designations and their respective stratigraphic layers defined in-field are listed in Table 1. Some of the stratigraphic designations used here differ slightly from those found in earlier publications (i.e., Koumouzelis et al., 2001a; Starkovich, 2009), because of revisions to the lithic industries (Kaczanowska et al., 2010).

Some aspects of the Middle Paleolithic from Klissoura Cave are still under study. Preliminary results from a large sample of lithics are available in Sitlivy et al. (2007; see also Koumouzelis et al., 2001a,b). There are currently no dates available for the earliest Middle Paleolithic deposits, though updated geoarchaeological data have linked these layers to marine oxygen isotope stages (MIS) (Karkanas, personal communication; Table 1). It is likely that the earliest layers formed during substages of MIS 5 and later Middle Paleolithic layers were deposited during MIS 4 or 3. During the warm phases of MIS 5, forests expanded through mainland Greece (Tzedakis, 1993, 1994, 1999; Tzedakis et al., 2002a; Wijmstra, 1969). MIS 4 saw forests contract and an expansion of open steppe

Table 1

Archaeological horizons and their corresponding cultural and chronological information. Number of identified specimen counts are included for each horizon. Dates from Koumouzelis et al., 2001a; Kuhn et al., 2010; Lowe et al., 2012. Changes from early versions reflect updated information, though dating of the Middle Paleolithic has yet to be resolved.

Culture	Layer	Years BP (cal)	MIS stage	NISP
Mesolithic	3–5a	^a 10,350 ± 800	1	256
Epigravettian	IIa–d	^a 17,150 ± 600	2	67
Mediterranean backed bladelet	III'	35,381 ± 690	3	1359
Non-Aurignacian UP	III''		3	1617
Aurignacian (upper)	IIIb–d	35,000–37,500	3	1158
Aurignacian (middle)	IIIe–g		3	1699
Aurignacian (lower)	IV		3	3110
Early UP (Uluzzian)	V	39,280 ± 110	3	246
Middle Paleolithic	VIII	53,637 ± 3135	3	1322
Middle Paleolithic	X		3	241
Middle Paleolithic	XI–XIV		3–5	1779
Middle Paleolithic	XV–XVII		5	2031
Middle Paleolithic	XVIII–XIX	>62,290 ± 3930	5	2199
Middle Paleolithic	XXa–XXb	>60,250 ± 2700	5	1106

^a Changes from earlier versions reflect updated information, though the dating of the Middle Paleolithic has yet to be resolved.

environments (Tzedakis, 1993, 1994, 1999; Tzedakis et al., 2002b). Though data from this period are currently not available for Peloponnese, southern Greece likely experienced a milder form of these changes. Geoarchaeological and preliminary dating evidence indicates that older Middle Paleolithic layers (XXa–XXb, XVIII–XIX, and XIV) were deposited during warm periods of MIS 5 or 4 (Karkanas, personal communication). Middle Paleolithic layer XIII probably formed during MIS 4 or 3, though this issue is not yet fully resolved.

Calibrated date ranges for the Upper Paleolithic and latest Middle Paleolithic layer appear in Table 1 (from Koumouzelis et al., 2001a,b; Kuhn et al., 2010; Lowe et al., 2012). The later Middle Paleolithic dates to at least 53,637 ± 3135 cal BP based on ABOX dating of wood charcoal. Middle Paleolithic layers XII–VIII and most of the Upper Paleolithic were deposited during MIS 3. Environmental conditions during these occupations oscillated between mixed forest-steppe plant communities, and warm, forested conditions, punctuated by some short periods of drying (Albert, 2010; Geraga et al., 2005; Karkanas, 2010; Ntinou, 2010; Tzedakis, 1999; Tzedakis et al., 2002b; Wijmstra, 1969).

Early Upper Paleolithic layer V is unique, as it contains arched-backed blades attributable to the Uluzzian period. To date, this is the only published example of the Uluzzian lithic industry in Greece, though this probably reflects the limited universe of available sites. The Uluzzian level is capped by a layer of tephra chemically sourced to the Campanian Ignimbrite eruption (Lowe et al., 2012), which dates to 39,280 ± 110 BP (De Vivo et al., 2001). This age serves as a minimum, but it is still several thousand years younger than recent dates from the Italian Uluzzian (Benazzi et al., 2011; Douka et al., 2014).

Radiocarbon dates on wood charcoal indicate that the Aurignacian was deposited between 37,500 and 35,000 cal BP (Kuhn et al., 2010). In general, the resolution of environmental data and dating evidence from the site during MIS 3 does not allow for correlations between specific archaeological layers and different climatic regimes, with the exception of Aurignacian layer IV. Macrobotanical and phytolith analyses indicate that layer IV was deposited during a slightly wetter period than other Upper Paleolithic levels (Albert, 2010; Ntinou, 2010). Faunal evidence supports the botanical data from this time, with an increase in species diversity in layer IV (Starkovich, 2012a). Wetter environments often correlate with increases in animal species diversity (Brown, 1975, 1973; Meserve and Glanz, 1978).

Aurignacian layers at Klissoura Cave 1 are quite thick, so they are divided into three groups: IV, IIIe–g, and IIIb–d (oldest to youngest). These groupings are based on stratigraphy, and do not reflect differences in stone tool technologies (Kaczanowska et al., 2010; Karkanas, 2010). Dividing the Aurignacian in this way is logical, however, because it allows for a higher-resolution look at these more intensively occupied layers. Aside from clear environmental differences during the formation of Aurignacian IV, it displays other unique attributes. One is a circular, anthropogenic rock alignment that is 1.5–2 m in diameter (Koumouzelis et al., 2001a; Stiner, 2010; Stiner et al., 2010). This structure is defined by a circle of large limestone rocks, dark staining within its confines, a lack of hearths, and a concentration of lithic debitage and ornaments inside of the alignment. The faunal signature of Aurignacian IV is also distinct, which is expanded upon below.

Above the Aurignacian lie two technologically distinct Upper Paleolithic backed bladelet or blade industries (III" and III', oldest to youngest). These deposits, as well as the Aurignacian layers, contain over fifty clay-lined hearths (Karkanas et al., 2004; Koumouzelis et al., 2001a; Pawlikowski et al., 2000). The features are currently unique to Klissoura Cave 1, and represent the oldest documented use of clay in the world. To construct the hearths, clay was brought from outside the site and formed into shallow basins. Analyses of the hearths indicate that they were cleaned after use, so it is unclear what they were used for (Pawlikowski et al., 2000). It is possible that they were satellite hearths, or surfaces for braising meat or parching plant materials.

At the end of MIS 3, environments in Greece continued to dry as steppe vegetation expanded across the region. This persisted until the last glacial maximum (Geraga et al., 2005; Kotthoff et al., 2008; Okuda et al., 1999; Turner and Sánchez-Goni, 1997; Tzedakis, 1999; Tzedakis et al., 2002b), and corresponds to a depositional hiatus at Klissoura Cave 1. This trend occurred in southern Greece until after 15,000 BP (Albert, 2010; Geraga et al., 2005; Karkanas, 2010; Kotthoff et al., 2008; Ntinou, 2010). Dates on soil carbonates place the Epigravettian at Klissoura Cave 1 to 17,150 ± 600, during this period of dry, open environments (Koumouzelis et al., 2001a). Mesolithic groups occupied the site in the early Holocene, when modern Mediterranean-type plant communities spread across Greece and there was an expansion of forests (Geraga et al., 2005; Hughes et al., 2006; Kotthoff et al., 2008; Lawson et al., 2005, 2004; Okuda et al., 1999; Turner and Sánchez-Goni, 1997; Tzedakis, 1994, 1993; Tzedakis et al., 2002b). Soil carbonates from the Mesolithic layers date to 10,350 ± 800 cal BP. Though dates on soil carbonates are often problematic, the chronology of the Epigravettian and Mesolithic at Klissoura Cave 1 are consistent with contemporary sites in the region.

4. Methods

Nearly 25,000 vertebrate specimens from the Klissoura Cave 1 faunal series were identified, representing an almost complete analysis of the assemblages. Certain samples, specifically those presented in a preliminary analysis of the Upper Paleolithic layers (Koumouzelis et al., 2001a, 2001b; Tomek and Bocheński, 2002) were excluded due to differences in sampling and recording methodology, though these early studies provided valuable contributions to the current research. Sampling was conducted for the Aurignacian units, and some of the larger Middle Paleolithic layers, though a large subset (>80%) was analyzed fully. Results reported here from the Early Upper Paleolithic/Uluzzian layer (V) are slightly larger than those mentioned elsewhere (i.e., Starkovich and Stiner, 2010; Starkovich, 2012a, 2011, 2009) because additional materials were discovered in storage after the initial analysis. Due to differences in occupation intensity and sediment erosion in certain

layers, as well as variation in the extent of excavation units depending on their depth, faunal sample sizes from different layers vary. The Mesolithic (3–5a), Epigravettian (IIa–d), Early Upper Paleolithic/Uluzzian (V) and Middle Paleolithic (X) layers all have fairly small samples (Table 1). Microfauna is extremely rare in the assemblage and is therefore excluded from this study.

Faunal analysis followed standard zooarchaeological methods and counting units (Grayson, 1984; Lyman, 1994; Reitz and Wing, 2008; Stiner, 2005). Number of identified specimens (NISP) is the basic counting unit from which minimum number of elements (MNE) is derived. Specimens are identified to the greatest precision possible (e.g., genus and species), or to body size class (e.g. medium or large ungulate) with less diagnostic fragments. Other observations were recorded for each specimen, including butchery and burning evidence, non-human taphonomic damage, epiphyseal fusion, tooth wear and eruption stages, and maximum specimen length. Macroscopically, bone preservation on the faunas is quite good, and most specimens are easily identifiable though they are highly fragmented. Weathering damage is rare, and a lack of carnivores and gnawed bones indicate that denning was uncommon at the site (Starkovich, 2011; Starkovich and Stiner, 2010). Evidence of raptor digestion is also absent from small mammals and bird remains, and the skeletal representation combined with fragmentation rates of bird bones suggests that they were not deposited at the site as raptor pellets (Bocheński and Tomek, 2010).

I now briefly discuss the potential destruction of faunal remains at the site, before outlining analyses designed to specifically test different foraging theory models at Klissoura Cave 1.

4.1. Density-mediated attrition

Density-mediated attrition is a well-known problem in zooarchaeology, as spongy elements and portions of elements are more susceptible than compact elements to destruction by carnivores, sediment compaction, and weathering (Binford and Bertram, 1977; Brain, 1981; Davis, 1987; Fisher, 1995; Lyman, 1994; Marean and Spencer, 1991). Following Lyman (1994, 1984), bone survivorship was calculated and compared to bone density values derived from photon densitometry measurements. Fallow deer was used for this analysis, since it is the most abundant taxa through the entire Klissoura Cave 1 sequence. Less diagnostic elements assigned to the category "medium ungulate" were combined with fallow deer data, as they most likely come from this species. Bone density standards applied to fallow deer are from American deer (*Odocoileus* sp.), the most closely-related taxon from which density standards are available. Correlation values between percent survivorship and bone density are presented in Table 2. Four layers are excluded from the analysis due to prohibitively small sample sizes. In the Upper Paleolithic, only Aurignacian layer IIIe–g displays a significant positive relationship between percent survivorship and bone density, though r_s^2 values indicate that density-mediated processes explain no more than five percent of variation in element representation (Table 2). The situation in the Middle Paleolithic is slightly more problematic. There is a positive correlation between bone density values and percent survivorship in all layers, with density-mediated attrition explaining 6–26% of the total variation in survivorship (Table 2). However, evidence for density-mediated attrition does not indicate the underlying cause of the bias (i.e., human or non-human processes). Human transport decisions or butchery patterns can also explain element bias in an assemblage.

A second method of evaluating density-mediated attrition that attempts to circumvent issues of transport or butchery involves the ratio between ungulate tooth and skull part MNE (following Stiner,

Table 2

Spearman's rank-order correlation values for the relationship between bone mineral density and percent survivorship for fallow deer and medium ungulate remains by layer. Note that layers with small samples are excluded from the analysis. Asterisks indicate statistically significant correlations.

Layer	N	r_s	r_s^2	p
Med. Backed-bladelet (III')	80	0.04	0.00	0.74
Non-Aurig. UP (III'')	80	0.08	0.01	0.46
Aurignacian (upper) (IIIb–d)	80	0.04	0.00	0.76
Aurignacian (middle) (IIIe–g)	80	*0.22	0.05	0.05
Aurignacian (lower) (IV)	80	0.15	0.02	0.17
MP (VIII)	82	*0.044	0.19	0.00
MP (XI–XIV)	82	*0.36	0.13	0.00
MP (XV–XVIII)	82	*0.24	0.06	0.03
MP (XVIII and XIX)	82	*0.40	0.16	0.00
MP (XXa–XXb)	82	*0.51	0.26	0.00

1994:99–103). It is expected that when carcasses are brought to a site, teeth should remain with the skull, resulting in a roughly 1:1 ratio between the elements based on MNE. Overall, bones are more vulnerable to attritional processes than teeth because of differences in the mineral component of the two materials (70% for bone and 95% for tooth enamel) (Currey, 1984; Hillson, 2005; Lyman, 1994:72, 79). Therefore, a bias toward the preservation of teeth would indicate that attritional processes had affected an assemblage. Ratios of ungulate tooth to bone-based cranial MNE for “problematic” layers (those mentioned previously that display density-mediated attrition) are presented in Table 3. All ungulate taxa are included for a more robust dataset (see Starkovich, 2011, Appendix C for the full data). Almost all of the layers have a near-even ratio of tooth to cranial bone-based MNE, with the exception of Middle Paleolithic layer VIII, which has over a 2:1 ratio between the elements (Table 3). Based on these two methods of analysis, only layer VIII displays clear evidence for density-mediated attrition potentially affecting the remains. Therefore, we can be confident that trends in faunal use reflect real, human decisions regarding hunting strategies or site use, as opposed to being an artifact of preservation.

4.2. Prey choice

Multiple approaches are employed to evaluate prey choice through the occupation of Klissoura Cave 1. Number of identified specimen counts for the full spectrum of prey species from the site are available in Starkovich (2011). Taxa are divided into eight prey categories based on body size and behavior: four different sizes of ungulates, small and large carnivores, small slow-moving game, and small fast-moving game (Table 4). Following the tenets of the prey choice model, it is predicted that human foragers would rank these groups of animals according to differences in their handling costs and return rates, with large-bodied ungulates being the most preferable. Carnivores are afforded their own categories because

Table 3

Ratios between ungulate tooth and bone-based MNE for archaeological layers displaying significant correlations between bone mineral density and percent survivorship. Only Middle Paleolithic layer VIII displays an extreme bias toward tooth-parts compared to crania.

Layer	Tooth MNE	Bone MNE	Tooth:bone MNE
Aurignacian (middle) (IIIe–g)	11	10	1.10
Middle Paleolithic (VIII)	16	6	2.67
Middle Paleolithic (XI–XIV)	20	23	0.87
Middle Paleolithic (XV–XVII)	9	11	0.82
Middle Paleolithic (XVIII and XIX)	9	22	0.41
Middle Paleolithic (XXa–XXb)	11	9	1.22

Table 4

List of taxa divided by prey group as used in this text. Predicted rankings are included. Mass values from Nowack (1999) and Silva and Downing (1995).

	Weight range (kg)	Average mass (kg)	Prey ranking
Very large ungulate			
Aurochs (<i>Bos primigenius</i>)	500–1000	750.0	High
Large ungulate			
European wild ass (<i>Equus hydruntinus</i>)	200–260	230.0	High
Red deer (<i>Cervus elaphus</i>)	75–340	207.5	High
Wild pig (<i>Sus scrofa</i>)	50–350	200.0	High
Medium ungulate			
Ibex (<i>Capra cf. ibex</i>)	35–150	92.5	High
Fallow deer (<i>Dama dama</i>)	40–100	70.0	High
Small ungulate			
Chamois (<i>Rupicapra rupicapra</i>)	24–50	37.0	High
Roe deer (<i>Capreolus capreolus</i>)	15–50	32.5	High
Large carnivore			
Brown bear (<i>Ursus arctos</i>)	70	70.0	
Leopard (<i>Panthera pardus</i>)	28–90	59.0	
Wolf (<i>Canis lupus</i>)	25–38	31.5	
Small carnivore			
Eurasian lynx (<i>Lynx lynx</i>)	8–38	23.0	
Red fox (<i>Vulpes vulpes</i>)	8–10	9.0	
Wild cat (<i>Felis silvestris</i>)	3–8	5.5	
Stone/Pine marten (<i>Martes foina/M. martes</i>)	0.8–2.3	1.6	
Small, fast-moving			
Great bustard (<i>Otis tarda</i>)	10–16	13.0	Low
European hare (<i>Lepus europaeus</i>)	1.3–7.0	4.2	Low
Rock partridge (<i>Alectoris graeca</i>)	0.51–0.68	0.6	Low
Small, slow-moving			
Tortoise (<i>Testudo</i> sp.)	1–2+	1.5	Medium

they are behaviorally different than herbivores, and have a higher potential for being introduced to the site through non-anthropogenic means. The small, slow-moving category is comprised of tortoises (*Testudo* sp.), while the small, fast-moving group includes European hare (*Lepus europaeus*) and birds (primarily rock partridge, *Alectoris graeca*, and great bustard, *Otis tarda*). Small birds (<0.1 kg) and unidentifiable snakes were excluded from the groupings because it is not clear that they were introduced to the site by humans. However, they exist in extremely low frequencies (NISP <15 in the entire assemblage), so their inclusion would likely have little effect on the final interpretations.

As is discussed in detail elsewhere (Starkovich, 2012a), the main small game species at Klissoura Cave 1 have drastically different life history characteristics, predator evasion tactics, and in some cases, habitat requirements. The points relevant to this discussion are briefly summarized here. Environmental factors are deemphasized because it was argued previously that shifts in small game occurred irrespective of local environmental changes at this particular site (Starkovich, 2012a). In fact, three of the four small game species (tortoise, rock partridge, and European hare) are poor climatic indicators because they are so flexible in their habitat requirements (Arnold and Burton, 1992; Cramp, 1980; Handrinos and Akriotis, 1997; Mitchell-Jones et al., 1999; Nowack, 1999; Vavalekas et al., 1993). The fourth small taxon, great bustard, does require more open habitats to accommodate its large wingspan (Cramp, 1980; Heinzel et al., 1992; Johnsgard, 1991). Indeed, fluctuations in great bustard frequencies probably relate to environmental change (Starkovich, 2012a), though shifts in the overall use of small game is not driven by this single taxon (see below).

Tortoises are extremely slow terrestrial animals that are easily collected by human foragers of all ages. They have low capture costs and high return rates, so they are expected to be a preferred class of prey whenever they are available (Stiner et al., 2000). In addition, their life history characteristics are unique, making them rather sensitive indicators of shifts in human foraging strategies. As

reptiles, tortoises continue to grow throughout their lifetimes. This growth is slow, however, so they take a long time to reach reproductive maturity. Tortoises display sexual size dimorphism, with females typically larger than males (Blasco et al., 1986–87; Hailey and Loumbourdis, 1988; Lambert, 1981; Swingland and Stubbs, 1985). This unique combination of features means that the largest, most obvious individuals on the landscape are mature females that form the reproductive base of the population (Stiner et al., 2000). Therefore, tortoises can tolerate low-level predation by hominins, but more intensive harvesting can lead to population depression or even local extinction. A decline in the frequency of tortoises in an archaeological sequence might indicate over-exploitation by human foragers.

Great bustards are categorized here with birds as small, fast-moving animals, though their relatively large size potentially provides higher return rates than hares or partridges. Like tortoises, bustards have low reproductive and developmental rates, and rely disproportionately on the success of older females (Morales et al., 2002). Though females over six years of age have twice the reproductive rates as younger birds, they average only 0.40 chicks per year and generally do not breed two years in a row (Morales et al., 2002). Population turnover is low and successful females tend to be long-lived. Like tortoises, bustards are quickly stressed with the removal of members of their reproductive base and succumb to population depression rather easily.

Rock partridges and European hares have the lowest return rates of the species found at Klissoura Cave 1. This is because they provide a small nutritional package, and have rapid flight responses when facing predation. However, both species are prolific and reproduce in the first years of life. Hares give birth to up to four litters per year with five leverets per birth (Burton, 1991), while partridges have yearly clutch sizes of twelve to eighteen eggs (Vavalekas et al., 1993). The high reproductive rates of these two taxa allow them to handle heavy predation fairly readily. Partridges and hares are nearly seven times more productive as compared to Mediterranean tortoises (Stiner et al., 2000).

In this study, proportions of small game animals are considered relative to one another, and the entire group is compared to large game taxa. The rationale behind these comparisons is that hominins should preferentially hunt large game, followed by small, slow animals, and should only turn to small, fast prey once the former categories are eliminated or are rare in the environment.

4.3. Central place foraging

Examining the representation of prey body parts at an archaeological site is crucial to understanding decisions surrounding the transport of prey to a base camp or habitation site, assuming post-depositional factors did not greatly impact the composition of the assemblage. A bias toward high-utility skeletal portions at Klissoura Cave 1 may indicate an increase in travel time between the site and hunting locations. Conversely, a lack of such bias could indicate a strategy involving the local hunting of game. It is important to also consider different motivations in the movement of carcass portions. For example, a strategy exclusively involving meat procurement might lead to the movement of different skeletal elements than transport based on maximizing bone marrow stores.

There are many different methods for examining prey transport decisions by past hunters (e.g., Binford, 1978; Broughton, 1999; Faith and Gordon, 2007; Stiner, 1991). One is based on utility indices introduced by Binford (1978) from his work with the Alaskan Nunamiut. Binford derived a baseline set of data that provides nutritional utility indices for meat, bone marrow, and bone grease from different skeletal elements of caribou (*Rangifer tarandus*) and domestic sheep (*Ovis aries*). Two combined indices

were calculated from the tissue-specific values: the general utility index (GUI) and modified general utility index (MGUI). The former considers the three classes of animal tissue by element, and the latter provides normalized values for each bone, taking into account low-utility portions that tend to be transported as “riders” along with food-rich elements. Binford (1978) then presented a set of utility curves that examine the relationship between MGUI and the frequency of different skeletal parts in an assemblage as predictive models for understanding Nunamiut transport decisions. These models were quickly adopted by zooarchaeologists (e.g., Landals, 1990; Speth, 1983; Thomas and Mayer, 1983), though criticisms related to methodological (Chase, 1985; Jones and Metcalfe, 1988; Metcalfe and Jones, 1988) and taphonomic (Grayson, 1989; Lyman, 1985) concerns soon emerged. Though the original transport models are no longer used, comparisons between utility indices and skeletal part frequency are still commonly applied in faunal studies.

Skeletal part frequencies are determined by calculating minimal animal units (MAU) (Binford, 1978). The observed MNE for a particular element is divided by the expected MNE value for the same element in a complete skeleton. It is then converted to %MAU by dividing the previous value by the maximum MAU value in the assemblage: (observed MNE/expected MNE)/(maximum MAU). As with the analysis of density-mediated attrition, this calculation was only applied to fallow deer and “medium ungulate” axial elements (raw data available in Starkovich, 2011, Appendix I). Percent MAU was calculated for each of the stratigraphic layers with sufficiently large sample sizes (fallow deer NISP > 100). Binford's (1978) utility index values for caribou were then compared to the fallow deer data. Caribou was chosen because, as a cervid, it is the closest species to fallow deer for which utility values are available. Positive correlations between %MAU and the meat index, GUI, or MGUI might indicate transport strategies that focus on meat-rich elements, while a correlation between %MAU and the marrow index could indicate preferential transport seeking to optimize fatty bone marrow returns.

An additional method for interpreting transport strategies by human predators was introduced by Broughton (1999), and evaluates mean utility at a site. The method employs the food utility index (FUI), which is a simplified version of Binford's (1978) caribou MGUI derived by Metcalfe and Jones (1988). Following Broughton (1999), mean FUI values are calculated for fallow deer in each archaeological layer at Klissoura Cave 1 by multiplying fallow deer MNE for each element by the element's respective FUI value. Values for all elements are then summed, and divided by the total MNE for the layer to determine mean FUI. This is then compared to the average FUI for a complete skeleton to determine if hominins were selectively transporting high- or low-utility parts, and whether or not there is a temporal trend in transport strategies. Note that Broughton (1999) used an NISP-based value for his comparison while MNE is preferred in this study.

4.4. Patch choice

As discussed above, the extent to which a carcass is processed for its edible tissues is one possible measure of resource intensification. The patch choice model predicts that foragers utilize the highest-return tissues first, and low-return animal products are only exploited if their processing costs are lower than the combined travel and handling costs for additional prey items. A shift in bone marrow processing patterns is therefore used as a marker for intensification at the site. Cold bone marrow processing is a labor-intensive activity compared to the butchery of meat and organs, but it is still quite simple. Using a hammerstone, marrow-bearing bones are crushed, granting foragers access to highly nutritious marrow

cavities (e.g., Binford, 1978; Blumenschine and Selvaggio, 1991; Brain, 1981; Stiner, 1994, 2005). This level of processing is nearly ubiquitous at Paleolithic sites from all time periods and regions, starting as early as the Lower Paleolithic (Binford, 1984; Boyle, 2000; Brain, 1981; Costamagno et al., 2006; Egeland and Byerly, 2005; Gaudzinski-Windheuser and Niven, 2009, and discussion therein; Hockett and Bicho, 2000; Miracle, 2005; Niven, 2007; Stiner, 1994, 2005, among many others).

In order to assess variation in the degree of cold marrow processing at Klissoura Cave 1, medium ungulate long bones were ranked by the volume of their marrow cavities (following Stiner, 2005; see also Binford, 1978 for bone marrow index values). Large ungulates were not considered because of small sample sizes. In almost all cases, marrow-bearing bones larger than the calcaneus were broken, with the exception of only one intact calcanei from layer III'. The remaining elements include phalanges, which are the lowest-ranked of the marrow-bearing bones. Phalanx marrow cavities differ in size, with first phalanges containing the greatest amount of marrow and terminal phalanges the least. It is expected that phalanges richer in marrow should be processed more frequently than those poor in marrow. It follows that when resources are intensified, foragers should break bones containing the smallest amount of marrow (e.g., terminal phalanges) at higher frequencies. Therefore, changes in the proportion of complete versus processed phalanges are used as a marker of intensification in this study.

Potential explanations for increases in processing intensity include environmental factors as well as human population growth. Lupo et al. (2013) point out that processing intensity should have an inverse relationship with environmental productivity because foragers can spend less time on an individual patch (or carcass) if other prey items are readily available (see also Burger et al., 2005). In order to test the relationship between environmental productivity and processing intensity, correlations between the reciprocal of Simpson's Index and percent of opened terminal phalanges are explored. The reciprocal of Simpson's Index is a standard biological measurement of species evenness in an environment (Simpson, 1949). At Klissoura Cave 1 there is no temporal trend in reciprocal of Simpson's Index values when all species are considered. In general, higher values are thought to represent more favorable environmental conditions at the site (see Starkovich, 2012a for discussion and values used here). A negative correlation is expected

between the two variables if occupants of the site intensively processed phalanges for marrow when environmental conditions were less favorable. Relationships between processing intensity and time are also examined to test diachronic trends in bone marrow extraction.

5. Results

5.1. Prey choice

In testing shifts in subsistence strategies using the prey choice model, changes in the representation of different species and prey groups are evaluated for Klissoura Cave 1. Fig. 2 depicts the abundance of each of the prey categories by layer. Medium ungulates dominate for most of the sequence, though large ungulates attain increased importance in Aurignacian layer IV. This reflects greater overall ungulate species diversity during a wetter phase of site occupation (Albert, 2010; Ntinou, 2010; Starkovich, 2012a). Small, fast-moving game animals become the most abundant prey category during the Epigravettian and Mesolithic.

Prey choice is analyzed quantitatively through the sequence by comparing changes in the proportions of large and small game (combining the slow and fast prey categories). Shifts in the frequency of small game is calculated using the following simple index: $(\text{NISP small game})/(\text{NISP small game} + \text{NISP large game})$. Raw data are presented in Table 5, and the representation of small game is graphed as a scatter plot against time in Fig. 3. Warm, mild, and cool phases of MIS curve are included on the top axis of the graph. As the dates for the Middle Paleolithic layers are still being determined, points are spread based on estimations and preliminary dating results (Karkanas, personal communication). Using a Spearman's rank-order correlation, the relationship between time period and proportion of small game is significant and positive ($r_s = 0.754$, $p = 0.002$). Cochran's test of linear trend, which is a chi-square-based tool that is less susceptible to both Type I and Type II errors, particularly where small samples are concerned (Cannon, 2001), was also utilized. The trend based on this statistic is also significant ($\chi^2_{\text{trend}} = 916.3$, $p < 0.001$). Small game clearly comprised a greater part of the diet in later time periods at the site.

Fig. 4 plots the relative frequency of small game by species throughout the sequence. Certain layers are excluded due to small sample sizes for small game (NISP < 25). Small, fast-moving

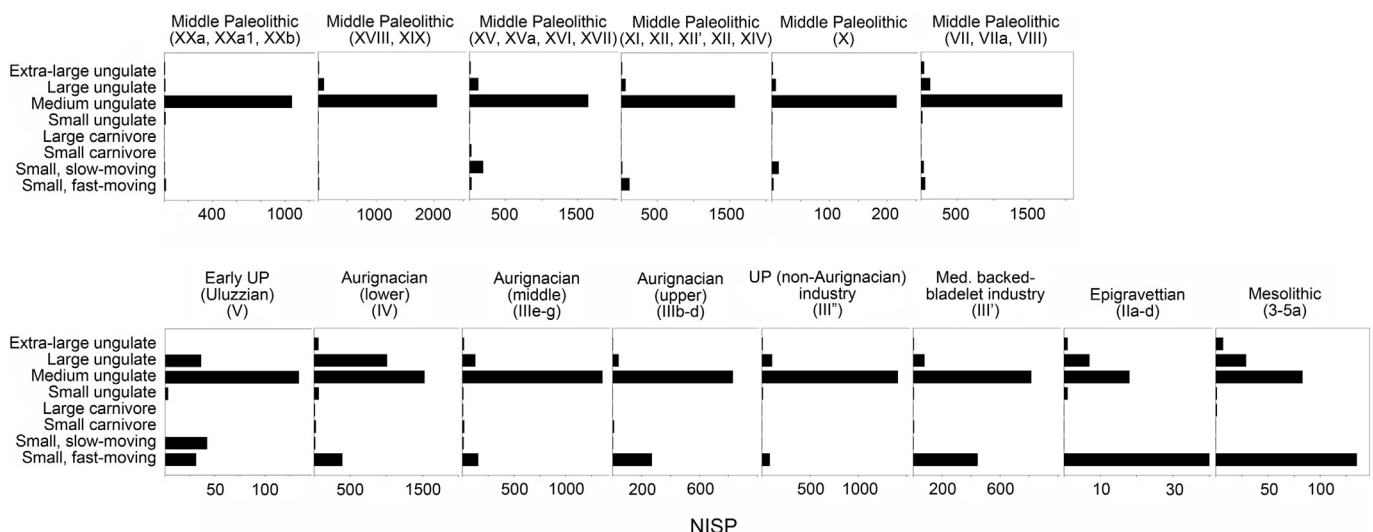


Fig. 2. Prey body types by layer, plotted by NISP.

Table 5

NISP counts and proportions of large and small game by layer. Small game is also split into counts of small slow and small fast animals.

Culture	Layer	Total NISP	Proportion of NISP		Small game NISP	Proportion of NISP	
			Small game	Large game		Small, slow	Small, fast
Mesolithic	3–5a	256	0.529	0.471	135	0.000	1.000
Epigravettian	IIa–d	67	0.597	0.403	40	0.000	1.000
Med. backed bladelet	III'	1359	0.331	0.669	443	0.007	0.993
Non-Aurignacian UP	III''	1617	0.051	0.949	82	0.012	0.988
Aurignacian (upper)	IIIb–d	1158	0.239	0.761	270	0.011	0.989
Aurignacian (middle)	IIIe–g	1699	0.095	0.905	158	0.076	0.924
Aurignacian (lower)	IV	3110	0.133	0.867	397	0.042	0.958
Early UP (Uluzzian)	V	246	0.297	0.703	73	0.575	0.425
Middle Paleolithic	VII–VIII	2241	0.042	0.958	93	0.394	0.606
Middle Paleolithic	X	241	0.062	0.938	*15	0.800	0.200
Middle Paleolithic	XI–XIV	1779	0.072	0.928	128	0.117	0.883
Middle Paleolithic	XV–XVII	2031	0.108	0.892	215	0.870	0.130
Middle Paleolithic	XVIII–XIX	2199	0.011	0.989	*25	0.440	0.560
Middle Paleolithic	XXa–XXb	1106	0.015	0.985	*17	0.235	0.765

animals (i.e., European hare, rock partridge, and great bustard) are depicted using shades of gray and black to indicate their similar handling costs, while slow-moving animals (i.e., tortoises) are differentiated by white bars. Hares were hunted in all periods but their importance increased through time after the Uluzzian, though they are also common in one Middle Paleolithic layer (XI–XIV). Conversely, tortoises were significant only in the Middle Paleolithic and Uluzzian period, and disappear from the assemblages by the Epigravettian (Fig. 4). Rock partridges and great bustard are more important in the later Aurignacian layers (IIIb–d) and in Upper Paleolithic layer III', which might relate to drier, more open conditions in the area during these phases (Starkovich, 2012a). In general, the most productive small prey (i.e., hares and partridges), were used heavily by Upper Paleolithic and Mesolithic hunters, starting in the Aurignacian.

Another way to consider changes in small game use at Klissoura Cave 1 is to examine the proportion of small, fast-moving species to small, slow-moving species through time, using an index similar to the one described above: (NISP small fast)/(NISP small fast + NISP small slow). Data are included in Table 5 and the proportion of

small, fast-moving game animals is graphed as a scatter plot against time in Fig. 5, again removing the small samples mentioned previously. A Spearman's rank-order correlation between time period and the proportion of small, fast-moving game in the small game assemblage is significant and positive ($r = 0.952$, $p = 0.000$). Cochran's test of linear trend that includes all layers confirms this relationship ($\chi^2_{\text{trend}} = 672.2$, $p < 0.001$). Small, slow-moving animals were a more important part of the diet by NISP in the earlier time periods of Klissoura Cave 1, and were replaced by fast-moving small species during the Upper Paleolithic.

In addition to the vertebrate faunas, land snails (*Helix figulina*) were also exploited at Klissoura Cave 1, particularly during later time periods. Based on a sample of snails from two excavation units, it is clear that the number of snails in the deposits increase significantly with time. No snails are found in the Middle Paleolithic layers, and they are rare in the Uluzzian and lower parts of the Aurignacian (layers IV and IIIe–g). The few shells from these earlier Upper Paleolithic layers display no unambiguous evidence of human modification, while snail shells from later periods have broken aperture rims (73–95%), and are biased to mostly include large individuals (2.3–2.4 cm) (Starkovich and Stiner, 2010). Land snails are moderately abundant in the later Aurignacian (IIIb–d), increase dramatically in subsequent Upper Paleolithic layers (III' and III''), and peak in the Mesolithic. The Epigravettian, which has the smallest sample of vertebrate remains from the sequence, contains few snail shells, though species diversity is high (including *Rumina decollata*, *Lindholmiola cf. spectabilis*, and *Zonitidae* spp.) and representative of taxa found near the site (Starkovich and Stiner, 2010). The trend in land snail use seems to mirror that of the vertebrate faunas, with an overall expansion in diet breadth to include lower-ranked resources through the cultural sequence. Though land snails are not difficult to collect, the cooking and extraction of snail meat is fairly labor-intensive, considering their small size, so their return rates are quite low.

5.2. Central place foraging

The data presented in this section seek to determine the nature of hominin body part transport strategies at Klissoura Cave 1, and whether these strategies changed through time. All available animal tissues (i.e., meat, marrow, and grease) are considered to fully understand the movement of ungulate carcasses to the site, and how hominins used the site as a home base, or central place. Spearman's rank-order correlation values between fallow deer % MAU and Binford's (1978) utility indices are presented in Table 6. Full raw data are available in Starkovich (2011). Few correlations are

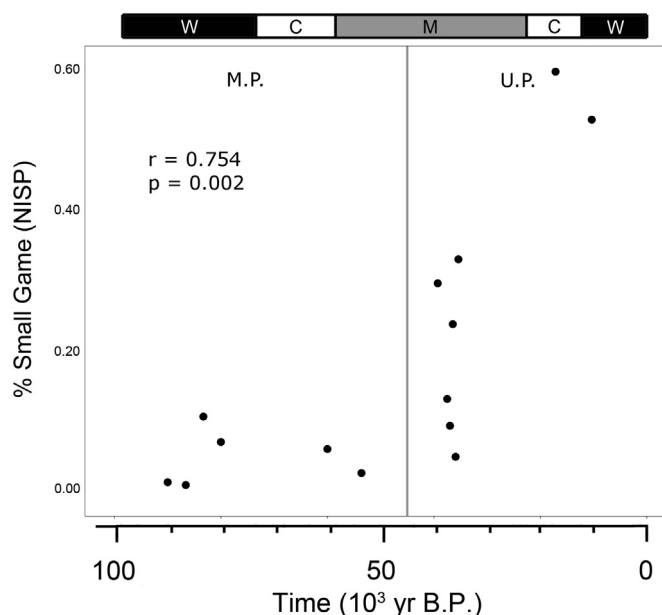


Fig. 3. Percentage of small game by NISP, plotted against time. The correlation is significant and positive (data from Table 5).

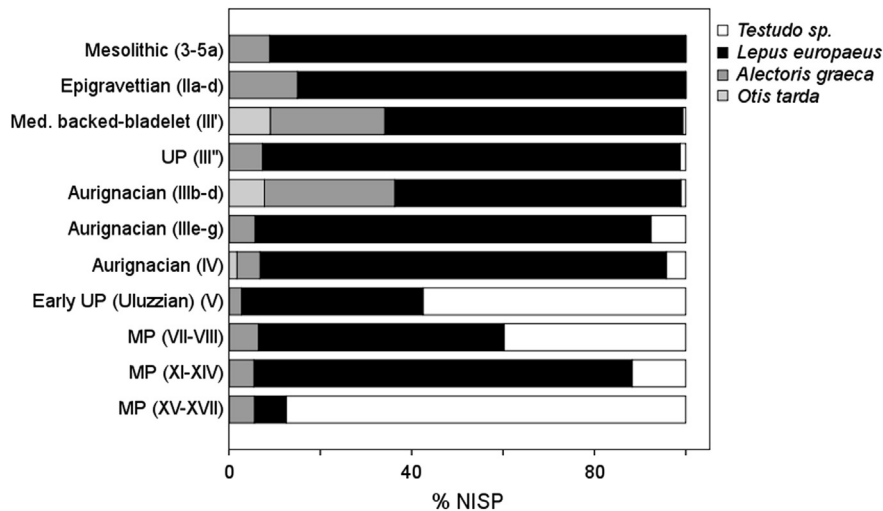


Fig. 4. Proportions of major small game taxa by layer. Some layers are excluded due to small sample sizes.

significant, with the exception of marrow index values in Aurignacian layer IV and Middle Paleolithic layer XXa–XXb (Table 6). It is possible that during these two phases nutrient-rich bone marrow was the goal of foraging excursions. This might be true, in particular, for Aurignacian layer IV, when ungulate bones were intensively processed for their marrow (see below). Overall, however, there is no preferential transport of high-utility elements. This is especially the case for Middle Paleolithic layer VIII, which has a significant, negative relationship between %MAU and both meat and GUI index values. As discussed previously, however, multiple lines of evidence indicate that density-mediated attrition was a potential factor in layer VIII.

Turning to an additional method of evaluating hominin transport strategies, mean FUI values for fallow deer are presented by layer in Table 7 and Fig. 6 (raw calculations in Starkovich, 2011, Appendix J). Only Middle Paleolithic layer XVIII–XIX has a higher mean FUI value than a complete skeleton, which might indicate

increased transport distances and the preferential movement of high-utility elements during this period. Middle Paleolithic VIII displays a particularly low mean FUI value compared to other layers; however, there is evidence for density-mediated attrition in this particular layer. There is no trend in average utility values through the sequence ($r_s = 0.042$, $p = 0.907$). Overall, there is no evidence for the selective movement of high utility elements at the site, suggesting that fallow deer were hunted near Klissoura Cave 1 in most phases of the occupation.

5.3. Patch choice

Major ungulate long bones were consistently opened for medullary marrow in all time periods at Klissoura Cave. However, there is variation in some of the smaller bones, phalanges in particular. Table 8 presents frequencies of opened phalanges by layer in assemblages with adequate sample sizes. In general, first phalanges were processed more often than second phalanges, which were in turn opened more frequently than terminal phalanges (Table 8, Fig. 7). This likely reflects differences in nutritional return: terminal phalanges contain the least amount of bone marrow, so they should be broken less frequently if processing was optimized.

Through the sequence, there is no correlation between the percent of opened terminal phalanges and time ($r_s = 0.176$, $p = 0.627$), though marrow processing was slightly less intense in the earliest and latest phases of the occupation (Fig. 7). There is also no relationship between opened terminal phalanges and biotic evenness as measured by the reciprocal of Simpson's Index ($r_s = 0.467$, $p = 0.174$). However, examining the data from the Middle and Upper Paleolithic separately does indicate some interesting relationships. There is a significant correlation between time and opened terminal phalanges during the Middle Paleolithic ($r_s = 0.900$, $p = 0.037$), which indicates increased processing intensity in the later parts of this phase. Conversely, in the Upper Paleolithic, there is a significant relationship between the reciprocal of Simpson's Index and opened terminal phalanges ($r_s = 0.900$, $p = 0.037$). This is counter to expectations set forth previously, that greater environmental productivity should be reflected in decreased processing intensity. Evidence for increases in site use at certain points in the Upper Paleolithic, however, might explain this unexpected relationship. Aurignacian layer IV, in particular, displays heavy processing of terminal phalanges.

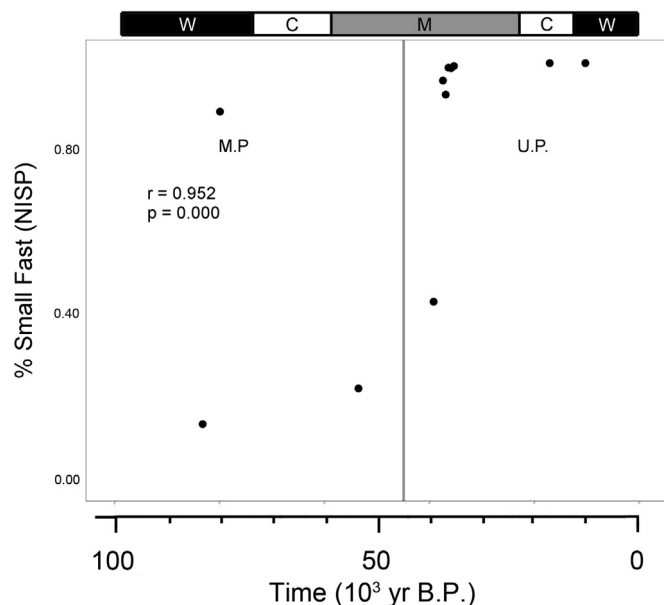


Fig. 5. Percentage of small, fast-moving game by NISP, plotted against time. The correlation is significant and positive (data from Table 5).

Table 6
Correlation values between %MAU and Binford's (1978) utility index values. Significant values are indicated by an asterisk. Double asterisks mark significant negative correlations.

	Meat			Marrow			Grease			GUI			%MGUI		
	r_s	r_s^2	p	r_s	r_s^2	p	r_s	r_s^2	p	r_s	r_s^2	p	r_s	r_s^2	p
Med. backed bladelet (III')	-0.103	0.011	0.611	-0.700	0.490	0.724	0.050	0.003	0.810	-0.130	0.017	0.519	0.021	0.000	0.916
UP (non-Aurignacian) (III'')	-0.190	0.036	0.343	-0.137	0.019	0.488	-0.291	0.085	0.150	-0.173	0.030	0.388	-0.085	0.007	0.668
Aurignacian (upper) (IIIb–d)	-0.251	0.063	0.206	-0.179	0.032	0.363	-0.058	0.003	0.780	-0.228	0.052	0.252	-0.170	0.029	0.388
Aurignacian (middle) (IIIe–g)	-0.041	0.002	0.838	0.102	0.010	0.607	0.072	0.005	0.728	-0.019	0.000	0.927	0.121	0.015	0.540
Aurignacian (lower) (IV)	-0.257	0.066	0.196	*0.507	0.257	0.006	0.257	0.066	0.206	-0.237	0.056	0.233	-0.093	0.009	0.639
Middle Paleolithic (VIII)	**−0.424	0.180	0.027	0.145	0.021	0.461	0.057	0.003	0.780	**−0.414	0.171	0.032	-0.294	0.086	0.129
Middle Paleolithic (XI–XIV)	-0.105	0.011	0.603	0.275	0.076	0.157	0.124	0.015	0.546	-0.103	0.011	0.608	0.046	0.002	0.815
Middle Paleolithic (XV–XVII)	-0.186	0.035	0.352	0.091	0.008	0.645	-0.107	0.011	0.604	-0.114	0.013	0.570	-0.142	0.020	0.471
Middle Paleolithic (XVIII–XIX)	-0.050	0.003	0.805	0.161	0.026	0.391	0.379	0.144	0.056	-0.031	0.001	0.879	0.080	0.006	0.684
Middle Paleolithic (XXa–XXb)	-0.336	0.113	0.087	*0.439	0.193	0.019	0.140	0.020	0.494	-0.318	0.101	0.106	-0.084	0.007	0.670

6. Discussion and conclusions

Following the predictions set forth by the prey choice model, lower-ranked resources are expected to enter forager diets when high-ranked resources become less abundant in the environment (Emlen, 1966; MacArthur and Pianka, 1966; Pianka, 2000; Stephens and Krebs, 1986). Decreases in the abundance of high-ranked resources can result from environmental change, human hunting pressures, or a combination of both. Widening diet breadth manifests as greater evenness in the proportion of prey types in an archaeological assemblage, or by the increased importance of low-ranked resources relative to high-ones.

A possible deviation from the prey choice model at Klissoura Cave 1 is the occasional appearance of hares in the Middle Paleolithic, particularly layers XI–XIV, where there are no other indications of resource stress. Hare is present, but rare, in the Middle Paleolithic of the site, with an MNI (minimum number of individuals) of one animal in most layers. Layer XI–XIV has a higher incidence of hare than other Middle Paleolithic layers (MNI = 2), but it is possible that some of these specimens are intrusive. There is no evidence of cut marks on the XI–XIV hare bones, and frequencies of burning on the remains are much lower than those for the overall assemblage from this layer (Starkovich, 2011). Early exploitation of small, fast-moving animals is observed at some sites from the western Mediterranean (e.g., Blasco and Peris, 2009; Sanchez Sera and Peris, 2008), so it is clear that Middle Paleolithic hominins were capable of exploiting these animals. However, at Klissoura Cave 1, hares never comprised a significant part of the diet in the Middle Paleolithic.

Overall, there is evidence for a long-term trend in resource depression and widening of diet breadths at Klissoura Cave 1. The proportion of hunted prey types changes through the sequence, favoring small, quick-types and labor-intensive invertebrates with

time, suggesting an overall increase in capture or handling costs relative to food yields. From the Middle Paleolithic through Mesolithic at the site, foragers shifted their hunting efforts from large to small game, the lowest-return, fast-moving animals in particular. Starkovich (2012a) tested the hypothesis that shifts in environmental conditions explain changes in game use in the Klissoura Cave 1 sequence. Though ungulate species diversity and the abundance of certain small game taxa (i.e., great bustard) do indeed correlate with changes in local vegetation, overall trends in species use occurred independent of environmental change. From these lines of evidence, it seems clear that resource depression and a subsequent widening of forager diets occurred at Klissoura Cave 1 over the course of the Late Pleistocene through Early Holocene.

Central place foraging models seek to explain the transport decisions foragers make when bringing resources to a home base (Orians and Pearson, 1979; Schoener, 1979). It is expected that, if humans exploit large game near a home base or habitation site, they will move both high and low-utility elements because the cost of transporting large portions of a carcass is fairly low. This would result in a more even anatomical representation at a site. Conversely, if foragers travel long distances to hunt, returns are maximized by only bringing high-utility elements back to a habitation site. Shifts in transport strategies that result in an increase in high-utility elements might reflect changing environmental conditions or local overhunting.

Table 7

Mean FUI values for fallow deer by layer, alongside the average value for a complete cervid skeleton. Bold values indicate an average FUI higher than the mean for a complete skeleton.

Layer	Mean FUI
Med. Backed-bladelet (III')	1604
Non-Aurig. UP (III'')	1520
Aurignacian (upper) (IIIb–d)	1529
Aurignacian (middle) (IIIe–g)	1663
Aurignacian (lower) (IV)	1513
MP (VIII)	1227
MP (XI–XIV)	1593
MP (XV–XVIII)	1517
MP (XVIII and XIX)	1792
MP (XXa–XXb)	1540
Complete skeleton	1762

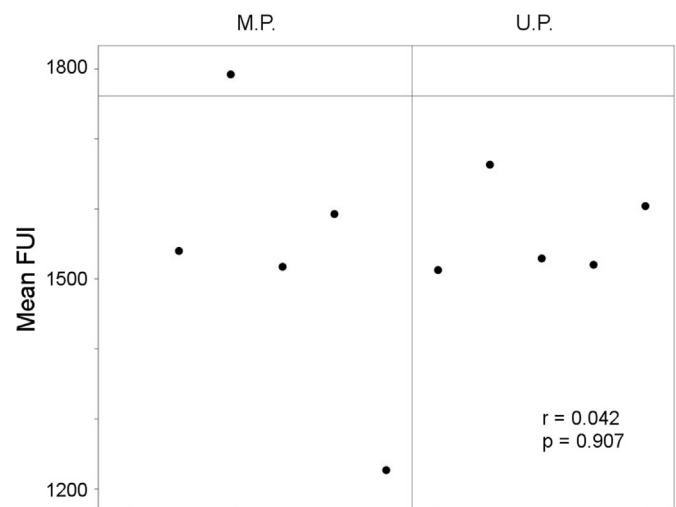


Fig. 6. Mean FUI by layer, following Broughton (1999). Horizontal line indicates the average FUI for a complete cervid. Data from Table 7. Note the lack of a significant temporal trend.

Table 8
Percentage of unopened phalanges by layer.

Layer	1st phalanx	2nd phalanx	3rd phalanx
Med. backed bladelet (III')	5.9	41.7	46.2
UP (non-Aurignacian) (III'')	7.4	16	71.4
Aurignacian (upper) (IIIb–d)	0	42.9	61.5
Aurignacian (middle) (IIIe–g)	0	5	57.9
Aurignacian (lower) (IV)	5.7	0	20.8
MP (VIII)	4.8	0	55.6
MP (XI–XIV)	0	8.3	33.3
MP (XV–XVII)	2.9	0	58.3
MP (XVIII–XIX)	0	13.3	64
MP (XXa–XXb)	13.3	22.2	69.2

An evaluation of prey body parts indicates that there is no diachronic trend in transport decisions at Klissoura Cave 1 through its occupation. Further, in all layers except for one, the mean utility of the recovered elements is less than the average utility for a complete cervid carcass. The lack of trend and general presence of lower-utility body parts suggests the local procurement of game throughout the occupation. Correlations between Binford's (1978) utility indices and survivorship in the different layers indicates that bone marrow was a possible motivating factor in the movement of elements in Aurignacian layer IV and Middle Paleolithic layer XXa–XXb. Similar patterns are found in western Europe (e.g., Morin, 2012:210; Niven, 2007), so it seems that nutrition-rich bone marrow was often a key goal in Paleolithic foraging efforts.

Though species abundance data provide clear evidence for resource depression and intensification at the site, a lack of trend in body part profiles implies that Klissoura Cave 1 hominins did not solve this problem by increasing the distance traveled to forage. Rather, it seems that large game animals were hunted locally, perhaps as they passed through the gorge or drank from the nearby stream. Long-distance hunting was not the only option available to foragers in southern Greece when faced with resource depression. In fact, there is a point where the travel distance necessary to procure large game is so great, that it is probably more energetically efficient to hunt small animals locally (Cannon, 2003).

The patch choice model was derived for predicting the patches a forager will exploit on a landscape (MacArthur and Pianka, 1966). The most relevant anthropological application of patch choice

models to the analysis presented here is to the butchery or processing intensity of prey carcasses. In this instance, resource intensification is reflected in bone marrow processing over time, which can indicate resource stress from human population pressures (Burger et al., 2005; Nagaoka, 2005). Changes in processing intensity might be in response to seasonal or long-term shortages, or the more intensive occupation of a particular site.

At Klissoura Cave 1, marrow processing of major ungulate long bones was high throughout the occupation. Elements with the lowest stores of bone marrow (especially terminal phalanges), have the potential to provide more sensitive information about intensive marrow processing at the site. Based on this metric, carcass processing intensified over the course of the Middle Paleolithic, though this trend did not continue into the Upper Paleolithic. By the Upper Paleolithic, marrow processing correlates closely with species diversity and favorable environmental conditions. This is counter to predictions set forth by Lupo et al. (2013), who postulates that processing time should vary inversely with environmental productivity. At Klissoura Cave 1, this relationship is largely driven by extremely high frequencies of terminal phalanx processing in Aurignacian layer IV, which formed during a wet phase with diverse ungulate populations available in the area. There is also a preference for the transport of marrow-rich elements to the site at this time. Other lines of evidence, including high quantities of lithics, ornaments, and hearth structures, point to an increase in site use at this time. Taken with the faunal evidence, it seems that foragers intensively exploited the rich local environment near Klissoura Cave 1 at the beginning of the Aurignacian, and while the occupation was intensive enough to increase carcass processing and change transport goals, it did not impact prey populations in a measurable way.

The application of models from evolutionary ecology to understand the foraging behaviors of hominins occupying Klissoura Cave 1 provides important insights about prey choice, transport decisions, and butchering intensity at the site, and how these behaviors changed through the sequence. Overall, trends in faunal exploitation fit fairly well with those found at other Late Pleistocene sites in the Mediterranean (e.g., Atici, 2009; Costamagno and Laroulandie, 2004; Munro, 2004; Speth and Clark, 2006; Stiner and Munro, 2011; Stiner, 2009, 2005; Stiner et al., 2000, 1999; Tortosa et al., 2002), but there are also differences that reflect local environmental conditions and unique features of site use. The shift from high-ranked large game to low-ranked small animals parallels the situation elsewhere, including other sites in Greece (e.g., Franchthi Cave), where Mesolithic foragers turned their attention to low-ranked animals such as hares, birds, and especially fish (Payne, 1975; Stiner and Munro, 2011). While other areas in the Mediterranean saw a temporal trend in carcass processing intensity (e.g., Portugal and the Levant: Bar-Oz and Munro, 2005, 2007; Manne and Bicho, 2009; Munro, 2004, 2009), Klissoura Cave 1 hominins did not uniformly contend with resource depression in this way. Instead, increases in carcass processing and shifts in transport goals appear to reflect temporary increases in site use. The data presented in this paper largely support the hypotheses proposed above, that resource intensification at the site occurred on multiple scales in response to both temporary changes in site use, and also larger demographic pressures in southern Greece throughout the Late Pleistocene.

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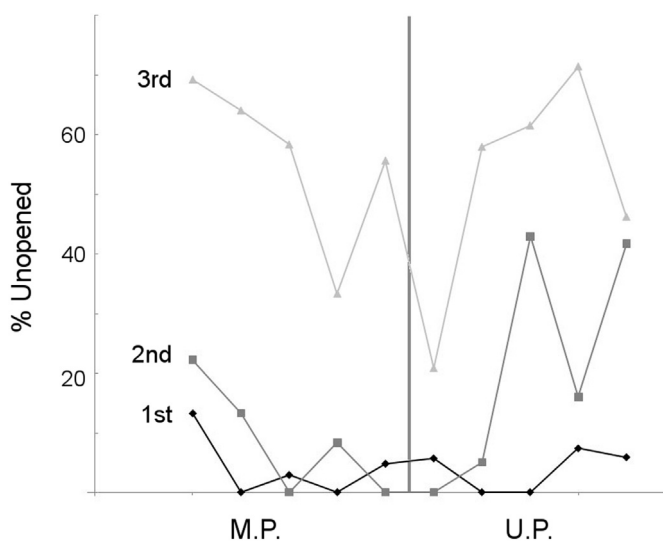


Fig. 7. Percentage of unopened first, second, and third phalanges by layer. Third phalanges contain the smallest amounts of bone marrow. Data from Table 8.

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